Overlooked model uncertainties may misinform forest management strategies

Victor, Jérôme, Isabelle

Forests play a major role in mitigating climate change, but they must be carefully managed to maintain this role through increasing anthropogenic threats. Robust management requires robust forecasts, but current projections are the outcome of layered models and highly variable. Identifying the drivers of this variability—whether it is from different emissions scenarios, uncertainty in climate models or ecological models—is thus critical to advancing management. To address this, we compare over 1350 ecological models and climate scenarios in forecasts for forests across Europe. Our approach considers a gradient of more mechanistic ('process-based') to correlative models of species distributions. We find that difference between ecological models represent the largest source of uncertainty (40 to 64%), surpassing both climate models and vastly different climate scenarios (e.g., SSP2 vs. SSP5). We also find areas with relatively consistent projections where management could take immediate action. Our results point to current limitations in ecological forecasting methods that make management difficult. At the same time they provide a framework to identify regions with the most consistent projections and those regions where high ecological uncertainty, which may benefit from diversified and more risk-adverse strategies until ecological forecasting advances.

Main

14

21

Forests are key to climate change mitigation policies and achieving carbon neutrality ^{1,2}. Yet, forests are increasingly under pressure. In Europe, temperatures are rising twice as fast as the global average³, and unprecedented pulses of tree mortality have been reported in the last decade⁴. As a result, some European forests are becoming net CO₂ sources^{5,6}, due to decreased growth ^{5,7}, larger burned areas ^{8,9}, and increased pest- and drought-induced dieback ^{6,10,11}.

Forest managers working to minimize current threats while also promoting long-term adaptation to climate change rely on forecasts of shifts in critical tree species. Species shifts are predicted to have major impacts on timber production and on the forest economic sector ^{12,13}. To preserve the socio-economic functions of forests, managers need to know whether the current species will be able to tolerate future climate conditions, whether they can rely on natural regeneration, or whether they should consider new species opportunities. To date, however, ecological models have struggled to provide practical insights for forest management.

Different models, ranging from correlative to more mechanistic approaches, often provide highly divergent projections ^{14–17}. While it remains unclear under which conditions one approach is more reliable than another ¹⁸, most projections still rely on a limited set of models ^{19,12,13,20}, masking significant uncertainties and ultimately increasing the risk of policy and management failures ²¹.

To incorporate the current reality of uncertain forecasts, forest managers require better information on the processes that cause uncertainty. Current projections have several layers of climatological and biological uncertainties, including socioeconomic scenarios, global climate models, ecological models, down to the species level. If the main driver of variation across

projections is the differences between ecological models, even more than different global emissions scenarios, it becomes critical to encompass a wide range of models. Failing to do so could lead to overly confident predictions about which species will or will not be able to survive in future climates, ultimately leading to counterproductive or even detrimental forest management decisions. Consistency between projections can also reveal regions where models agree and where uncertainty is lower.

To this aim, we combined over 1350 projections from models of future forest tree species distributions (from 1970 to 2100, at a 0.1° spatial resolution). We incorporated a wide range of ecological models, from more mechanistic ('process-based') to correlative models to 'hybrid' models. To forecast from these models we also considered climate model variability (5 global climate models with different climate sensitivities) and two emissions ('forcing') scenarios, resulting in 10 different future climate simulations. Our dataset included 9 tree species, both deciduous and coniferous, adapted to diverse climatic conditions across Europe.

Including variability from the ecological, climatological and emissions scenarios allowed us to quantify the contribution of each component to the total variation across projections. This approach represents a significant advancement over previous studies, which overlooked large portions of uncertainty. Such advances could lead to more informed decision-making to improve the resilience of forests.

Results and discussion

29

30

36

37

47

51

61

64

Differences between ecological models consistently explained more variation than vastly different climate trajectories. Overall, we found that the choice of the ecological model explained 51% of the variation across species and biomes, while uncertainty in the socio-economic pathway explained only 35% of the variations (Figure 1). The current driest biome, the Mediterranean region, showed a consistent decline in suitability across all species. The Atlantic and Continental biomes displayed contrasting results depending on the species. Few of the detected trends were significant, however, due to the large total uncertainty (Figure 1). One striking example is the climatic suitability change of sessile oak in the Atlantic region, where this species represents an important cultural and economic value, and for which more than 80% of the uncertainty in climate change impact projections was due to variations among ecological models.

Subheader: Mechanistic to correlative models contribute to high uncertainty ...

Accounting for more diverse ecological models led to a more comprehensive range of potential future change in suitability (Figure 2), revealing the high divergence between ecological models and the persistent gaps in our understanding of species responses to climate change. Considering only correlative models would have misled to an overestimation of the contribution of climate projections (forcing scenarios, climate models, and their two-way interaction) to the total projection uncertainty in all regions, except the Mediterranean. In particular, divergence between climate models would have appeared to contribute as much as ecological models to projection uncertainty (on average, 36.6% and 37.5%, respectively).

Using a comprehensive set of models allows to avoid the specific biases inherent to some modeling approaches. Our results revealed that models calibrated using current species range data consistently predict greater extinctions than models calibrated using experimental data (Figure 3). Current distribution data may capture only a portion of the climatic niche of a species, underestimating the range of conditions where it could survive 22,23 . These discrepancies between models can significantly alter country-level projections, and impact national strategies derived from them. For example, by the end of the 21st century, beech showed an average suitability decrease of -0.19 (± 0.14) across its historical distribution when considering only models entirely calibrated with current species distribution data, leading to an average loss of 30.5% of its historical distribution (Figure 3). But this decreasing trend vanishes once a broad range of models is accounted for (-0.028 ± 0.17). Relying on a narrow set of models—especially

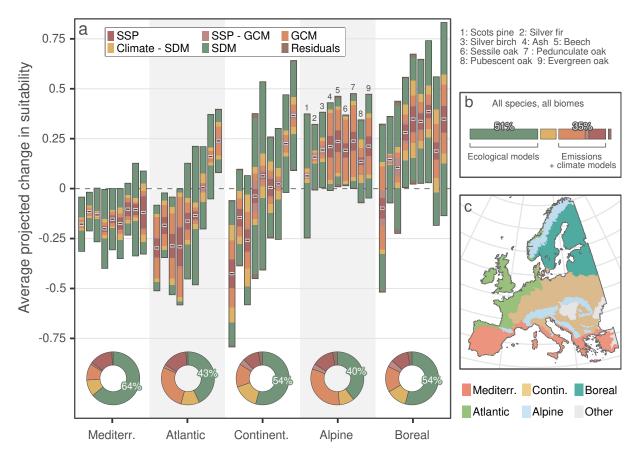


Figure 1: Ecological models represent the main source of uncertainty in future projections of species climatic suitability across European biomes (2080-2100). This figure illustrates the level of uncertainty associated with projected changes in suitability relative to the historical period (1970–2000), (a) for each species within biome and (b) across all species and biomes. We distinguish 5 main uncertainty sources: (i) the future scenario (SSP), (ii) the climate model used to generate the climate projections (GCM), (iii) the interactions between the SPP and the GCM, (iv) the species distribution modeling method (SDM), and (v) the interactions between SDM and climate projections (both GCMs and SSPs). For each species, the black line represents the mean projection, across all GCMs, SSPs, and SDMs. 90% uncertainty ranges were calculated additively and symmetrically around the mean.

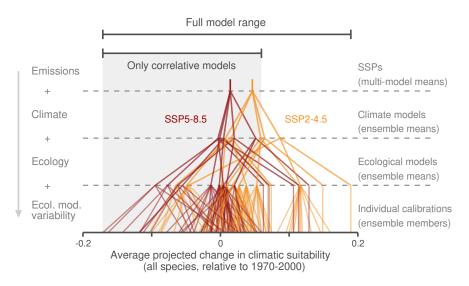


Figure 2: Considering a broad range of models provides a more comprehensive view of possible future scenarios. This figure illustrates the average change in suitability across all species and all biomes, with the hirarchical contribution of each source of uncertainty. The top of each cascade represents the overall average change in suitability for each SSP. The level below shows the ensemble mean for each climate model (5 branches per SSP, corresponding to the 5 GCMs considered here), averaged across multiple ecological models. The next level represents the contribution of each ecological modeling approach (mechanistic, hybrid, and correlative, 3 branches per GCM). The final level displays the variations within each approach (e.g., different parameter calibrations or statistical algorithms), although for mechanistic models only a single calibration was available. This figure was inspired by the Figure 1.15 in IPCC, 2021: Chapter 1.

derived from the same calibration process—undermines the robustness of projections ²¹, and may ultimately bias decisions towards intensive intervention strategies (e.g. introduction of species outside their native range), potentially overlooking alternative strategies.

Subheader: Moving forward with management despite uncertainties

74

7.5

76

80

81

83

84

87

88

89

90

91

92

Despite large uncertainties, comparing diverse models improve prediction robustness and enable to identify areas with relatively consistent projections where precise actions for adaptation can be decided with larger confidence (Figure 4). Around the Mediterranean Basin, the models consistently predict less favorable climatic conditions for the species we considered here. In areas where most species are threatened, forest managers may thus consider introducing more drought-tolerant species. Along the Atlantic margin, the suitability of most species is also projected to decrease, except for the two Mediterranean species—pubescent and evergreen oaks— which could replace less adapted temperate species such as beech²⁴. Mechanistic model projections are less pessimistic for deciduous oaks and beech (Figure 3), suggesting that some better-adapted populations could survive if the existing standing genetic variation is maintained and promoted by forest managers²⁵. Additionally, adapting management practices, such as decreasing stand density to limit competition for water, could support their long-term survival to drought events²⁶. Finally, boreal biomes in Scandinavian and Baltic countries are projected to get an overall increase of climatic suitability (Figure 4). These include Finland and Sweden, two very important forestry countries in terms of wood stock, added value, and forest-based workforce [cite]. Forests in these regions are dominated by two conifers species, Scots pine and spruce, favoured by commercial forest management. Insufficient experimental data prevented us from making mechanistic model projections for spruce, but uncertainty for Scot pine future suitability was very high. Models consistently project that temperate deciduous trees will become more competitive at the northern margin of their range (Figure 3), and the extending growing season could offer an opportunity to convert pure coniferous stands into mixed forest to increase their resilience 27 .

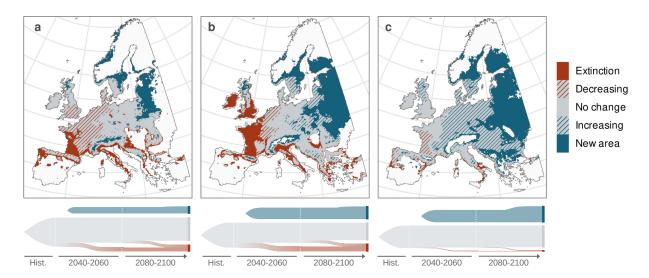


Figure 3: Models build on current species range data project higher extinctions. This figure illustrates the average projection of beech distribution under scenario SSP2-4.5, for each of the 3 ecological modeling approaches considered here: **(a)** correlative, **(b)** hybrid and **(c)** mechanistic models. The upper maps show the projected change in beech distribution for 2080–2100, relative to its historical distribution (1970-2000). The lower Sankey diagrams illustrate the temporal evolution of beech distribution, from its historical distributions to projected distributions for 2040–2060 and 2080–2100.

Our framework also allow to identify regions of high uncertainty, highlighting where diversification strategies are most required. A large part of the Continental biome exhibit less clear trends (Figure 4), as well as mountainous regions at the transition between Mediterranean and Continental/Atlantic climates (Pyrenees, Massif Central, Balkans). A key lever of action in this region is the diversification of tree species, as well as increasing genetic diversity within populations, to mitigate the risks associated with uncertain future conditions ^{28–31}. Promoting uneven-aged stands could also enhance forest stability by improving structural complexity and buffering against climate extremes ^{32,33}.

100

104

106

108

114

118

123

124

Even in these highly uncertain regions our approach still highlights some smaller zones of consistency. Models agree on a lower suitability for Scots pines (with uncertainty driven more by climatic models and scenarios, 45.7%, than by ecological models, 30.8%), which is a commercially very important species [cite] in several countries of Central Europe (such as Poland, Eastern Germany, Czech Republic, Belarus). Projections also suggest that temperate deciduous species (e.g. beech, deciduous oaks) will be less affected by climate change, despite high uncertainties due to high divergence among ecological models (between 45.7 and 75.4% of the total uncertainty).

Subheader: Advancing on two fronts: move forward with uncertainty while aiming to reduce it through improved ecological models

The implications of these results extend beyond European forests. Mechanistic models have also been developed for North America and Asia^{34,35}. Their projections could be systematically integrated in a comprehensive framework such as ours, alongside correlative model projections. Such continental-scale uncertainty assessment—going beyond regional analyses³⁶—would provide more robust guidance for forest management. This is particularly critical in countries where forests are managed at a broader scale than in Europe—such as the United States—and where it could thus be easier to incorporate uncertainty into large-scale decision making.

Given the rapid pace of climate change, rather than debating over which modeling approach to favor, efforts should focus on bridging diverse methodologies to generate practical insights and support evidence-based decision making. Ultimately, as scientists, we need to be transparent about projection uncertainties if we expect forest managers to acknowledge and integrate them ³⁷. This is how ecological modeling can become truly relevant to decision making in the face of a

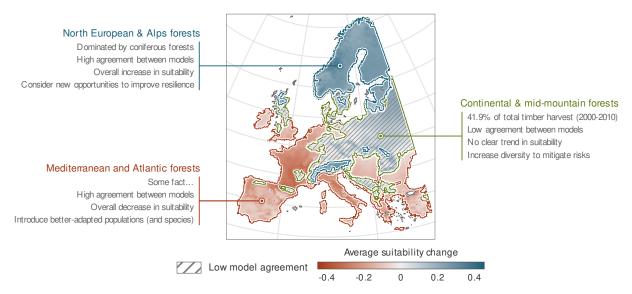


Figure 4: Accounting for uncertainties supports evidence-based forest management. Our framework allows to identify 3 areas that differ in terms of uncertainty levels, future climate risks and levers of action to address them.

changing climate.

Such an approach does not preclude continuing to improve ecological models to reduce their uncertainty. The large uncertainties we found clearly raise questions about the robustness of existing projections, and highlight that further advances are necessary to provide the most useful projections for managers and for policy. Correlative models are becoming more mechanistic by integrating experimental data ³⁸—yet, with some caution ³⁹. Combining deep learning with physics-based models offers a promising approach to improve climate predictions ⁴⁰, with a lower computational cost that could facilitate a more comprehensive estimation of uncertainties. These breakthroughs are continually enhancing our ability to make robust ecological and climatological forecasts, and could in turn reveal new innovative pathways for forest management. But the need for this improvement should not prevent us from providing a better framework to identify uncertainty in projections that can guide management, such the framework we offer here.

Methods

Species distribution models

We sought to encompass a broad diversity of species distribution models by including three different approaches: correlative models, mechanistic models and hybrid models (i.e. mechastic models calibrated like correlative models ⁴¹).

For the correlative approach, we selected four well-established models ⁴²: GLM with lasso regularization, GAM, BRT, and down-sampled Random Forest. For the mechanistic approach, we used the process-based model PHENOFIT. The model has been validated for several North American and European species, either in historical or Holocene climatic conditions ^{34,43–45,18}. For the hybrid approach, we calibrated PHENOFIT using the same species occurrence data as correlative models ⁴¹. We optimized the parameters of the model using the covariance matrix adaptation evolution strategy ⁴⁶.

Cliamte projections

Future simulations were run with the last Coupled Model Intercomparison Project Phase 6 (CMIP6) climate projections, for 5 global climate models (GCMs) and 2 shared socio-economic

pathways (SSPs). We used model projections that were downscaled to a 0.1° resolution with a statistical trend-preserving method (the cumulative distribution function transform), using the ERA5-Land reanalysis as a reference observational dataset between 1981 and 2010⁴⁷. The five GCMs were GFDL-ESM4⁴⁸, IPSL-CM6A-LR⁴⁹, MPI-ESM1-2-HR⁵⁰, MRI-ESM2-0⁵¹ and UKESM1-0-LL⁵². They are considered as good representatives of the full CMIP6 ensemble⁴⁷.

Uncertainty partitioning

161

164

165

166

Our approach was inspired by the partitioning of uncertainties in climate projections initially developed by Hawkins and Sutton ^{53,54}, which was subsequently enhanced with additional methodologies ^{55,56}. Rather than using a simple variance decomposition approach, we perform an ANOVA-based variance decomposition to also estimate the importance of the two-way interaction effects. All analyses were performed in R ⁵⁷.

Across all species, we partitioned three sources of uncertainty: the climate projection uncertainty related to the different GCMs, SSPs, and their interaction, the species distribution modeling uncertainty related to the differents SDMs. We also considered the interactions between SDMs and climate projections (GCMs and SSPs). For each year, the suitability of a cell was considered as a 21-year moving average suitability (e.g. 2040-2060 for the year 2050). We then computed the difference of suitability with the historical suitability (c1970-2000). For each GCM and each SSP, when multiple SDM projections were simulated within the same SDM approach (e.g. multiple algorithms for correlative approach), we kept one ensemble per approach. For each year t, we then applied a linear ANOVA to calculate the sums of squares attributable to each uncertainty source:

$$SS_{tot} = SS_{GCM} + SS_{SSP} + SS_{GCM:SSP} + SS_{SDM} + SS_{SDM:GCM} + SS_{SDM:SSP} + SS_{residuals}$$

We then computed 90% uncertainty ranges additively and symmetrically around the mean projection (across all GCMs, SSPs, SDMs), e.g. for SDM uncertainty: $\pm 1.645 * \sigma * \frac{SS_{SDM}}{SS_{tot}}$.

References

- [1] Anu Korosuo, Roberto Pilli, Raúl Abad Viñas, Viorel N. B. Blujdea, Rene R. Colditz, Giulia Fiorese, Simone Rossi, Matteo Vizzarri, and Giacomo Grassi. The role of forests in the EU climate policy: are we on the right track? Carbon Balance and Management, 18(1):15, July 2023. ISSN 1750-0680. doi: 10.1186/s13021-023-00234-0. URL https://doi.org/10.1186/s13021-023-00234-0.
- [2] Matti Hyyrynen, Markku Ollikainen, and Jyri Seppälä. European forest sinks and climate targets: past trends, main drivers, and future forecasts. European Journal of Forest Research, 142(5):1207–1224, October 2023. ISSN 1612-4677. doi: 10.1007/s10342-023-01587-4. URL https://doi.org/10.1007/s10342-023-01587-4.
- [3] Copernicus Climate Change Service. European state of the climate 2023. Technical report, 2024. URL https://climate.copernicus.eu/esotc/2023.
- [4] Cornelius Senf, Allan Buras, Christian S. Zang, Anja Rammig, and Rupert Seidl. Excess forest mortality is consistently linked to drought across Europe. *Nature Communications*, 11(1):6200, December 2020. ISSN 2041-1723. doi: 10.1038/s41467-020-19924-1. URL https://www.nature.com/articles/s41467-020-19924-1.
- [5] David Hadden and Achim Grelle. Changing temperature response of respiration turns boreal forest from carbon sink into carbon source. Agricultural and Forest Meteorology, 223:30–38, June 2016. ISSN 0168-1923. doi: 10.1016/j.agrformet.2016.03.020. URL https://www.sciencedirect.com/science/article/pii/S0168192316302131.
- [6] D. V. Karelin, D. G. Zamolodchikov, A. V. Shilkin, S. Yu. Popov, A. S. Kumanyaev, V. O. Lopes de Gerenyu, N. O. Tel'nova, and Michael L. Gitarskiy. The effect of tree mortality on CO2 fluxes in an old-growth spruce forest. European Journal of Forest Research, 140(2):287–305, April 2021. ISSN 1612-4677. doi: 10.1007/s10342-020-01330-3. URL https://doi.org/10.1007/s10342-020-01330-3.
- [7] Auke M. van der Woude, Wouter Peters, Emilie Joetzjer, Sébastien Lafont, Gerbrand Koren,
 Philippe Ciais, Michel Ramonet, Yidi Xu, Ana Bastos, Santiago Botía, Stephen Sitch,
 Remco de Kok, Tobias Kneuer, Dagmar Kubistin, Adrien Jacotot, Benjamin Loubet, PedroHenrique Herig-Coimbra, Denis Loustau, and Ingrid T. Luijkx. Temperature extremes of
 2022 reduced carbon uptake by forests in Europe. Nature Communications, 14(1):6218,
 October 2023. ISSN 2041-1723. doi: 10.1038/s41467-023-41851-0. URL https://www.
 nature.com/articles/s41467-023-41851-0.
- [8] Jofre Carnicer, Andrés Alegria, Christos Giannakopoulos, Francesca Di Giuseppe, Anna Karali, Nikos Koutsias, Piero Lionello, Mark Parrington, and Claudia Vitolo. Global warming is shifting the relationships between fire weather and realized fire-induced CO2 emissions in Europe. Scientific Reports, 12(1):10365, June 2022. ISSN 2045-2322. doi: 10.1038/s41598-022-14480-8. URL https://www.nature.com/articles/s41598-022-14480-8.
- [9] Julia Kelly, Natascha Kljun, Zhanzhang Cai, Stefan H. Doerr, Claudio D'Onofrio, Thomas Holst, Irene Lehner, Anders Lindroth, Shangharsha Thapa, Patrik Vestin, and Cristina Santín. Wildfire impacts on the carbon budget of a managed Nordic boreal forest. Agricultural and Forest Meteorology, 351:110016, May 2024. ISSN 0168-1923. doi: 10.1016/j. agrformet.2024.110016. URL https://www.sciencedirect.com/science/article/pii/S016819232400131X.

- [10] Emil Cienciala and Jan Melichar. Forest carbon stock development following extreme drought-induced dieback of coniferous stands in Central Europe: a CBM-CFS3 model ap-211 plication. Carbon Balance and Management, 19(1):1, January 2024. ISSN 1750-0680. doi: 212 10.1186/s13021-023-00246-w. URL https://doi.org/10.1186/s13021-023-00246-w.
- [11] Lejla Latifovic and M. Altaf Arain. The impact of spongy moth (Lymantria dispar 214 dispar) defoliation on carbon balance of a temperate deciduous forest in North Amer-215 Agricultural and Forest Meteorology, 354:110076, July 2024. ISSN 0168-1923. 216 doi: 10.1016/j.agrformet.2024.110076. URL https://www.sciencedirect.com/science/ 217 article/pii/S0168192324001916. 218
- [12] Johannes Wessely, Franz Essl, Konrad Fiedler, Andreas Gattringer, Bernhard Hülber, Ole-219 sia Ignateva, Dietmar Moser, Werner Rammer, Stefan Dullinger, and Rupert Seidl. A climate-induced tree species bottleneck for forest management in Europe. Nature Ecology & Evolution, 8(6):1109–1117, June 2024. ISSN 2397-334X. doi: 10.1038/s41559-024-02406-8. 222 $\mathrm{URL}\ \mathrm{https://www-nature-com.inee.bib.cnrs.fr/articles/s41559-024-02406-8}.$ 223
- [13] Marc Hanewinkel, Dominik A. Cullmann, Mart-Jan Schelhaas, Gert-Jan Nabuurs, and 224 Niklaus E. Zimmermann. Climate change may cause severe loss in the economic value of 225 European forest land. Nature Climate Change, 3(3):203-207, March 2013. ISSN 1758-6798. 226 doi: 10.1038/nclimate1687. URL https://www.nature.com/articles/nclimate1687. 227
- [14] Xavier Morin and Wilfried Thuiller. Comparing niche- and process-based models to reduce 228 prediction uncertainty in species range shifts under climate change. Ecology, 90(5):1301-1313, 2009. ISSN 1939-9170. doi: 10.1890/08-0134.1. URL https://onlinelibrary. 230 wiley.com/doi/abs/10.1890/08-0134.1. 231
- Trevor Keenan, Josep Maria Serra, Francisco Lloret, Miquel Ninyerola, and Santiago 232 Predicting the future of forests in the Mediterranean under climate change, 233 with niche- and process-based models: CO2 matters! Global Change Biology, 17(1): 234 565-579, 2011. ISSN 1365-2486. doi: 10.1111/j.1365-2486.2010.02254.x. URL https: //onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2010.02254.x.

237

- [16] Alissar Cheaib, Vincent Badeau, Julien Boe, Isabelle Chuine, Christine Delire, Eric Dufrêne, Christophe François, Emmanuel S. Gritti, Myriam Legay, Christian Pagé, Wilfried Thuiller, 238 Nicolas Viovy, and Paul Leadley. Climate change impacts on tree ranges: model in-239 tercomparison facilitates understanding and quantification of uncertainty. Ecology Let-240 ters, 15(6):533-544, 2012. ISSN 1461-0248. doi: 10.1111/j.1461-0248.2012.01764.x. URL 241 https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1461-0248.2012.01764.x. 242
- [17] Antti Takolander, Thomas Hickler, Laura Meller, and Mar Cabeza. Comparing future 243 shifts in tree species distributions across Europe projected by statistical and dynamic 244 process-based models. Regional Environmental Change, 19(1):251–266, January 2019. ISSN 1436-378X. doi: 10.1007/s10113-018-1403-x. URL https://doi.org/10.1007/ 246 s10113-018-1403-x. 247
- [18] Victor Van der Meersch, Edward Armstrong, Florent Mouillot, Anne Duputié, Hendrik 248 Davi, Frédérik Saltré, and Isabelle Chuine. Biological mechanisms are necessary to improve 249 projections of species range shifts. bioRxiv, 2024. doi: 10.1101/2024.05.06.592679. URL 250 https://www.biorxiv.org/content/early/2024/05/08/2024.05.06.592679. 251
- [19] Marcin K. Dyderski, Sonia Paz, Lee E. Frelich, and Andrzej M. Jagodzinski. How much 252 does climate change threaten European forest tree species distributions? Global Change Biology, 24(3):1150-1163, 2018. ISSN 1365-2486. doi: 10.1111/gcb.13925. URL https: 254 //onlinelibrary.wiley.com/doi/abs/10.1111/gcb.13925. 255

- [20] Silvio Schueler, Wolfgang Falk, Jarkko Koskela, François Lefèvre, Michele Bozzano, Jason Hubert, Hojka Kraigher, Roman Longauer, and Ditte C. Olrik. Vulnerability of dynamic genetic conservation units of forest trees in Europe to climate change. Global Change Biology, 20(5):1498–1511, 2014. ISSN 1365-2486. doi: 10.1111/gcb.12476. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12476.
- [21] Terence P. Dawson, Stephen T. Jackson, Joanna I. House, Iain Colin Prentice, and Georgina M. Mace. Beyond Predictions: Biodiversity Conservation in a Changing Climate. Science, 332(6025):53–58, April 2011. doi: 10.1126/science.1200303. URL https://www.science.org/doi/10.1126/science.1200303.
- 265 [22] Mathieu Chevalier, Olivier Broennimann, and Antoine Guisan. Climate change may reveal currently unavailable parts of species' ecological niches. *Nature Ecology & Evolution*, pages 1–13, May 2024. ISSN 2397-334X. doi: 10.1038/s41559-024-02426-4. URL https://www.nature.com/articles/s41559-024-02426-4.
- [23] D. Nogués-Bravo, S. Veloz, B. G. Holt, J. Singarayer, P. Valdes, B. Davis, S. C. Brewer,
 J. W. Williams, and C. Rahbek. Amplified plant turnover in response to climate change forecast by Late Quaternary records. Nature Climate Change, 6(12):1115-1119, December 2016. ISSN 1758-6798. doi: 10.1038/nclimate3146. URL https://www.nature.com/articles/nclimate3146.
- [24] Josep Peñuelas and Martí Boada. A global change-induced biome shift in the Montseny mountains (NE Spain). Global Change Biology, 9(2):131–140, 2003. ISSN 1365-2486. doi: 10.1046/j.1365-2486.2003.00566.x. URL https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1365-2486.2003.00566.x.
- 278 [25] Peter Brang, Peter Spathelf, J. Bo Larsen, Jürgen Bauhus, Andrej Bonccina, Christophe Chauvin, Lars Drössler, Carlos García-Güemes, Caroline Heiri, Gary Kerr, Manfred J. Lexer, Bill Mason, Frits Mohren, Urs Mühlethaler, Susanna Nocentini, and Miroslav Svoboda. Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. Forestry: An International Journal of Forest Research, 87 (4):492–503, October 2014. ISSN 0015-752X. doi: 10.1093/forestry/cpu018. URL https://doi.org/10.1093/forestry/cpu018.
- [26] Derek J. N. Young, Becky L. Estes, Shana Gross, Amarina Wuenschel, Christina Restaino,
 and Marc D. Meyer. Effectiveness of forest density reduction treatments for increasing
 drought resistance of ponderosa pine growth. *Ecological Applications*, 33(4), April 2023.
 ISSN 1939-5582. doi: 10.1002/eap.2854.
- 289 [27] Bastian Schauer, Simon Thorn, Markus Blaschke, and Thomas Kudernatsch. Conversion of
 290 pure spruce to mixed spruce beech stands: Effects on alpha and beta diversity of multiple
 291 taxonomic groups. Forest Ecology and Management, 545:121297, October 2023. ISSN
 292 0378-1127. doi: 10.1016/j.foreco.2023.121297. URL https://www.sciencedirect.com/
 293 science/article/pii/S0378112723005315.
- 294 [28] Xavier Morin, Lorenz Fahse, Claire de Mazancourt, Michael Scherer-Lorenzen, and Harald Bugmann. Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. *Ecology Letters*, 17(12):1526–1535, 2014. ISSN 1461-0248. doi: 10.1111/ele.12357. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12357.
- ²⁹⁹ [29] Christian Ammer. Diversity and forest productivity in a changing climate. New Phy-³⁰⁰ tologist, 221(1):50-66, 2019. ISSN 1469-8137. doi: 10.1111/nph.15263. URL https: ³⁰¹ //onlinelibrary.wiley.com/doi/abs/10.1111/nph.15263.

- [30] Hans Pretzsch. Genetic diversity reduces competition and increases tree growth on a Norway spruce (*Picea abies* [L.] Karst.) provenance mixing experiment. Forest Ecology and Management, 497:119498, October 2021. ISSN 0378-1127. doi: 10.1016/j.foreco.2021.119498. URL https://www.sciencedirect.com/science/article/pii/S0378112721005880.
- Sonja Vospernik, Carl Vigren, Xavier Morin, Maude Toïgo, Kamil Bielak, Gediminas 306 Brazaitis, Felipe Bravo, Michael Heym, Miren del Río, Aris Jansons, Magnus Löf, Arne 307 Nothdurft, Marta Pardos, Maciej Pach, Quentin Ponette, and Hans Pretzsch. Can mix-308 ing Quercus robur and Quercus petraea with Pinus sylvestris compensate for produc-309 tivity losses due to climate change? Science of The Total Environment, 942:173342, 310 September 2024. ISSN 0048-9697. doi: 10.1016/j.scitotenv.2024.173342. URL https: 311 //www.sciencedirect.com/science/article/pii/S0048969724034892. 312
- [32] Elia Vangi, Daniela Dalmonech, Elisa Cioccolo, Gina Marano, Leonardo Bianchini, Paulina F. Puchi, Elisa Grieco, Alessandro Cescatti, Andrea Colantoni, Gherardo Chirici, and Alessio Collalti. Stand age diversity (and more than climate change) affects forests' resilience and stability, although unevenly. *Journal of Environmental Management*, 366: 121822, August 2024. ISSN 0301-4797. doi: 10.1016/j.jenvman.2024.121822.
- 318 [33] Shengmin Zhang, Jörgen Sjögren, and Mari Jönsson. Retention forestry amplifies micro-319 climate buffering in boreal forests. *Agricultural and Forest Meteorology*, 350:109973, May 320 2024. ISSN 0168-1923. doi: 10.1016/j.agrformet.2024.109973.
- [34] Xavier Morin, Carol Augspurger, and Isabelle Chuine. Process-Based Modeling of Species' Distributions: What Limits Temperate Tree Species' Range Boundaries? *Ecology*, 88(9): 2280–2291, 2007. ISSN 1939-9170. doi: 10.1890/06-1591.1. URL https://onlinelibrary.wiley.com/doi/abs/10.1890/06-1591.1.
- Jing Fang, Herman H. Shugart, Feng Liu, Xiaodong Yan, Yunkun Song, and Fucheng Lv.
 Forcchn v2.0: an individual-based model for predicting multiscale forest carbon dynamics.
 Geoscientific Model Development, 15(17):6863–6872, September 2022. ISSN 1991-9603. doi: 10.5194/gmd-15-6863-2022.
- Isolar Matthews, Matthew Peters, Anantha Prasad, William D. Dijak, Jacob Fraser, Wen J. Wang, Brice Hanberry, Hong He, Maria Janowiak, Patricia Butler, Leslie Brandt, and Christopher Swanston. Multi-model comparison on the effects of climate change on tree species in the eastern u.s.: results from an enhanced niche model and process-based ecosystem and landscape models. Landscape Ecology, 32(7):1327–1346, June 2016. ISSN 1572-9761. doi: 10.1007/s10980-016-0404-8.
- 335 [37] Andrea Saltelli, Gabriele Bammer, Isabelle Bruno, Erica Charters, Monica Di Fiore, Em336 manuel Didier, Wendy Nelson Espeland, John Kay, Samuele Lo Piano, Deborah Mayo,
 337 Roger Pielke Jr, Tommaso Portaluri, Theodore M. Porter, Arnald Puy, Ismael Rafols,
 338 Jerome R. Ravetz, Erik Reinert, Daniel Sarewitz, Philip B. Stark, Andrew Stirling, Jeroen
 339 van der Sluijs, and Paolo Vineis. Five ways to ensure that models serve society: a man340 ifesto. Nature, 582(7813):482-484, June 2020. doi: 10.1038/d41586-020-01812-9. URL
 341 https://www.nature.com/articles/d41586-020-01812-9.
- [38] Tyler Wagner, Erin M. Schliep, Joshua S. North, Holly Kundel, Christopher A. Custer,
 Jenna K. Ruzich, and Gretchen J. A. Hansen. Predicting climate change impacts on poikilo therms using physiologically guided species abundance models. *Proceedings of the National Academy of Sciences*, 120(15), April 2023. ISSN 1091-6490. doi: 10.1073/pnas.2214199120.

- Mathieu Chevalier, Vincent Pignard, Olivier Broennimann, and Antoine Guisan. A cautionary message on combining physiological thermal limits with macroclimatic data to predict species distribution. *Ecosphere*, 15(7), July 2024. ISSN 2150-8925. doi: 10.1002/ecs2.4931.
- [40] Dmitrii Kochkov, Janni Yuval, Ian Langmore, Peter Norgaard, Jamie Smith, Griffin Mooers,
 Milan Klöwer, James Lottes, Stephan Rasp, Peter Düben, Sam Hatfield, Peter Battaglia,
 Alvaro Sanchez-Gonzalez, Matthew Willson, Michael P. Brenner, and Stephan Hoyer. Neural general circulation models for weather and climate. Nature, 632(8027):1060–1066, July
 2024. ISSN 1476-4687. doi: 10.1038/s41586-024-07744-y.
- Victor Van der Meersch and Isabelle Chuine. Estimating process-based model parameters
 from species distribution data using the evolutionary algorithm CMA-ES. Methods in
 Ecology and Evolution, 14(7):1808–1820, 2023. ISSN 2041-210X. doi: 10.1111/2041-210X.
 14119. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/2041-210X.14119.
- Roozbeh Valavi, Gurutzeta Guillera-Arroita, José J. Lahoz-Monfort, and Jane Elith. Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. *Ecological Monographs*, 92(1):e01486, 2022. ISSN 1557-7015. doi: 10.1002/ecm.1486. URL https://onlinelibrary.wiley.com/doi/abs/10.1002/ecm.1486.
- Frédérik Saltré, Rémi Saint-Amant, Emmanuel S. Gritti, Simon Brewer, Cédric Gaucherel, Basil A. S. Davis, and Isabelle Chuine. Climate or migration: what limited European beech post-glacial colonization? Global Ecology and Biogeography, 22(11):1217–1227, 2013. ISSN 1466-8238. doi: 10.1111/geb.12085. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/geb.12085.
- Anne Duputié, Alexis Rutschmann, Ophélie Ronce, and Isabelle Chuine. Phenological plasticity will not help all species adapt to climate change. Global Change Biology, 21(8): 3062-3073, 2015. ISSN 1365-2486. doi: 10.1111/gcb.12914. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12914.
- Julie Gauzere, Bertrand Teuf, Hendrik Davi, Luis-Miguel Chevin, Thomas Caignard,
 Bérangère Leys, Sylvain Delzon, Ophélie Ronce, and Isabelle Chuine. Where is the optimum? Predicting the variation of selection along climatic gradients and the adaptive
 value of plasticity. A case study on tree phenology. Evolution Letters, 4(2):109–123, 2020.
 ISSN 2056-3744. doi: 10.1002/evl3.160. URL https://onlinelibrary.wiley.com/doi/
 abs/10.1002/evl3.160.
- Nikolaus Hansen and Andreas Ostermeier. Completely Derandomized Self-Adaptation in Evolution Strategies. *Evolutionary Computation*, 9(2):159–195, June 2001. ISSN 1063-6560. doi: 10.1162/106365601750190398.
- Thomas Noël, Harilaos Loukos, Dimitri Defrance, Mathieu Vrac, and Guillaume Levavasseur. Extending the global high-resolution downscaled projections dataset to include CMIP6 projections at increased resolution coherent with the ERA5-Land reanalysis. Data in Brief, 45:108669, December 2022. ISSN 2352-3409. doi: 10.1016/j.dib.2022.108669. URL https://www.sciencedirect.com/science/article/pii/S2352340922008745.
- [48] J. P. Dunne, L. W. Horowitz, A. J. Adcroft, P. Ginoux, I. M. Held, J. G. John, J. P. Krasting, S. Malyshev, V. Naik, F. Paulot, E. Shevliakova, C. A. Stock, N. Zadeh, V. Balaji, C. Blanton, K. A. Dunne, C. Dupuis, J. Durachta, R. Dussin, P. P. G. Gauthier, S. M. Griffies, H. Guo, R. W. Hallberg, M. Harrison, J. He, W. Hurlin, C. McHugh, R. Menzel, P. C. D. Milly, S. Nikonov, D. J. Paynter, J. Ploshay, A. Radhakrishnan, K. Rand, B. G. Reichl, T. Robinson, D. M. Schwarzkopf, L. T. Sentman, S. Underwood,

H. Vahlenkamp, M. Winton, A. T. Wittenberg, B. Wyman, Y. Zeng, and M. Zhao. The GFDL Earth System Model Version 4.1 (GFDL-ESM 4.1): Overall Coupled Model Description and Simulation Characteristics. *Journal of Advances in Modeling Earth Systems*, 12(11):e2019MS002015, 2020. ISSN 1942-2466. doi: 10.1029/2019MS002015. URL https://onlinelibrary.wiley.com/doi/abs/10.1029/2019MS002015.

391

392

393

- [49] Thibaut Lurton, Yves Balkanski, Vladislav Bastrikov, Slimane Bekki, Laurent Bopp, Pas-396 cale Braconnot, Patrick Brockmann, Patricia Cadule, Camille Contoux, Anne Cozic, David 397 Cugnet, Jean-Louis Dufresne, Christian Éthé, Marie-Alice Foujols, Josefine Ghattas, Didier 398 Hauglustaine, Rong-Ming Hu, Masa Kageyama, Myriam Khodri, Nicolas Lebas, Guillaume 399 Levavasseur, Marion Marchand, Catherine Ottlé, Philippe Peylin, Adriana Sima, Sophie 400 Szopa, Rémi Thiéblemont, Nicolas Vuichard, and Olivier Boucher. Implementation of the 401 CMIP6 Forcing Data in the IPSL-CM6A-LR Model. Journal of Advances in Modeling Earth 402 Systems, 12(4):e2019MS001940, 2020. ISSN 1942-2466. doi: 10.1029/2019MS001940. URL 403 https://onlinelibrary.wiley.com/doi/abs/10.1029/2019MS001940. 404
- [50] W. A. Müller, J. H. Jungclaus, T. Mauritsen, J. Baehr, M. Bittner, R. Budich, F. Bunzel, M. Esch, R. Ghosh, H. Haak, T. Ilyina, T. Kleine, L. Kornblueh, H. Li, K. Modali, D. Notz, H. Pohlmann, E. Roeckner, I. Stemmler, F. Tian, and J. Marotzke. A Higher-resolution Version of the Max Planck Institute Earth System Model (MPI-ESM1.2-HR).
 Journal of Advances in Modeling Earth Systems, 10(7):1383-1413, 2018. ISSN 1942-2466. doi: 10.1029/2017MS001217. URL https://onlinelibrary.wiley.com/doi/abs/10.1029/2017MS001217.
- Urakawa, Hiroyuki Tusjino, Makoto Deushi, Taichu Tanaka, Masahiro Hosaka, Shokichi
 Yabu, Hiromasa Yoshimura, Eiki Shindo, Ryo Mizuta, Atsushi Obata, Yukimasa Adachi,
 and Masayoshi Ishii. The meteorological research institute earth system model version 2.0,
 mri-esm2.0: Description and basic evaluation of the physical component. Journal of the
 Meteorological Society of Japan. Ser. II, 97(5):931–965, 2019. doi: 10.2151/jmsj.2019-051.
- Alistair A. Sellar, Jeremy Walton, Colin G. Jones, Richard Wood, Nathan Luke Abra-418 ham, Miroslaw Andrejczuk, Martin B. Andrews, Timothy Andrews, Alex T. Archibald, 419 Lee de Mora, Harold Dyson, Mark Elkington, Richard Ellis, Piotr Florek, Peter Good, Laila Gohar, Stephen Haddad, Steven C. Hardiman, Emma Hogan, Alan Iwi, Christo-421 pher D. Jones, Ben Johnson, Douglas I. Kelley, Jamie Kettleborough, Jeff R. Knight, 422 Marcus O. Köhler, Till Kuhlbrodt, Spencer Liddicoat, Irina Linova-Pavlova, Matthew S. 423 Mizielinski, Olaf Morgenstern, Jane Mulcahy, Erica Neininger, Fiona M. O'Connor, Ruth 424 Petrie, Jeff Ridley, Jean-Christophe Rioual, Malcolm Roberts, Eddy Robertson, Steven 425 Rumbold, Jon Seddon, Harry Shepherd, Sungbo Shim, Ag Stephens, Joao C. Teixiera, Yongming Tang, Jonny Williams, Andy Wiltshire, and Paul T. Griffiths. Implementation of U.K. Earth System Models for CMIP6. Journal of Advances in Modeling Earth Systems, 12(4):e2019MS001946, 2020. ISSN 1942-2466. doi: 10.1029/2019MS001946. URL 429 https://onlinelibrary.wiley.com/doi/abs/10.1029/2019MS001946. 430
- Ed Hawkins and Rowan Sutton. The Potential to Narrow Uncertainty in Regional Climate Predictions. Bulletin of the American Meteorological Society, 90(8):1095-1108, August 2009. ISSN 0003-0007, 1520-0477. doi: 10.1175/2009BAMS2607.1. URL https://journals.ametsoc.org/view/journals/bams/90/8/2009bams2607_1.xml.
- Ed Hawkins and Rowan Sutton. The potential to narrow uncertainty in projections of regional precipitation change. *Climate Dynamics*, 37(1):407–418, July 2011. ISSN 1432-0894. doi: 10.1007/s00382-010-0810-6. URL https://doi.org/10.1007/s00382-010-0810-6.

- 55] Stan Yip, Christopher A. T. Ferro, David B. Stephenson, and Ed Hawkins. A Simple, Coherent Framework for Partitioning Uncertainty in Climate Predictions. *Journal of Climate*, 24(17):4634-4643, September 2011. ISSN 0894-8755, 1520-0442. doi: 10.1175/2011JCLI4085.1. URL https://journals.ametsoc.org/view/journals/clim/24/17/2011jcli4085.1.xml.
- bavid C. Lafferty and Ryan L. Sriver. Downscaling and bias-correction contribute considerable uncertainty to local climate projections in CMIP6. npj Climate and Atmospheric Science, 6(1):1–13, September 2023. ISSN 2397-3722. doi: 10.1038/s41612-023-00486-0. URL https://www.nature.com/articles/s41612-023-00486-0.
- [57] R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, 2024. URL https://www.R-project.org/.